Camelus thomasi Pomel, 1893, a possible ancestor of the one-humped camel?

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Members of the order Tylopoda are accepted to be emigrants from the western to the eastern hemisphere via the Bering Land Bridge (Thenius 1972). The time of their arrival in the Old World cannot be established exactly, but the earliest fossil remains of camelids from Asia date to the Middle Pliocene (Kozhamkulova 1986). From the fossil record it is clear that the Plio-Pleistocene witnessed the presence of several species in the Palaearctic region. At least one camelid species is known from Africa as early as the Upper Pliocene (Howell et al. 1969; Gentry and Gentry 1969).

Fossil camels of the genus Camelus Linnaeus, 1758 descend from Plio-Pleistocene forms of the genus Paracamelus Schlosser, 1903, recorded from localities in north-eastern China, north-western Mongolia, Tadzhikistan, and Kazakhstan (Kozhamkulova 1986). Toward the end of the Pleistocene, the genus Camelus already had disappeared from large parts of its former Eurasian distribution area. Though population numbers of Old World camelids continued to decline, it is a fact that in the course of the Holocene two domestic forms make their appearance, for which LINNAEUS (1758) proposed the names Camelus dromedarius Linnaeus, 1758 and Camelus bactrianus Linnaeus, 1758 to designate respectively the one-humped and the two-humped form. The wild ancestor of the latter, first described by Przewalski in 1883 (and named Camelus bactrianus ferus), is believed to survive in the wild in southwest Mongolia, Kansu, Tsinghai, and Sinkiang (HEPTNER et al. 1966; Grubb 1993). Recent investigations have shown that the hypothesis of an early third millennium BC centre of domestication of the two-humped camel in eastern Iran or in southern Turkmenistan (Compagnoni and Tosi 1978) cannot be maintained any longer, since there is no proof whatsoever, that the Holocene distribution area of the twohumped wild camel included this region (Peters and von Den Driesch 1997).

Certain authors consider the two-humped wild camel to be the common ancestor of the two domestic forms, Arabian and Bactrian camels being breeds of the same species (e.g. Herre and Röhrs 1973), though they may have originated from two different subspecies (Köhler 1981; Herre and Röhrs 1990). The common ancestry is based on the observation that (1) fertile offspring can be produced from mating one-humped and two-humped camels, (2) the embryos of the two forms have two hump primordia, which fuse in the dromedary during subsequent foetal development (Lombardini 1879) and (3) the fact that there was no evidence for the presence of a one-humped wild camel during Middle Pleistocene to Holocene times in the Afrolevantine region, for *Camelus thomasi* Pomel, 1893, a large camel species inhabiting North Africa and the southwestern Levant, was considered osteologically to belong to the lineage of Asiatic camels (Gautter 1966).

Arguments contradicting the hypothesis of the Arabian and the Bactrian camel representing one species include the differences in outer appearance, ecophysiological adaptations, and zoogeographic range of the two domestic forms and the fact that continued crossbreeding rapidly results in loss of fertility (Kolpakov 1935). It was assumed that domestic one-humped camels must have originated from a wild ancestor present in Arabia at some date prior to the 3rd millennium BC, because dromedary remains from archaeological contexts of younger date, for example from urban sites at the east coast of the Arabian Peninsula, probably represent domesticated animals (Hoch 1979; Uerpmann 1987).

In the past, research on the ancestry of domestic camels has been hampered by the general belief that postcranial elements of one-humped and two-humped animals could not be separated morphologically. Some distinguishing postcranial features have been discussed by Lesbre (1903) and Wapnish (1984), but the osteomorphology of the entire postcranial skeleton of the Arabian and Bactrian camel has only recently been covered in detail and on a statistical basis by STEIGER (1990). The results of this study have been used to check the taxonomic status of Camelus thomasi, probably the only species of wild camel that occurred during the Middle and Late Pleistocene in North Africa and the Levant. Though it was not possible to obtain the C. thomasi type specimens, collected from an Acheulian context at Ternifine (Algeria) and described by POMEL (1893), the Upper Palaeolithic camel bones recovered from site 1040 by members of the Combined Nubian Prehistory and Geological Campaign in northern Sudan, studied by GAUTIER (1966), could be re-analysed morphologically. As a result, the current opinion of C. thomasi being closely related to the two-humped camel must be rejected, because the available fossil material (distal humerus, distal radius-ulna, distal tibia, and calcaneus) exhibits features that are characteristic for the one-humped camel (see STEIGER 1990 for details), i.e. the more pronounced crista epicondyli lateralis in the humerus, the larger, more distally located medial epicondyle and the more concave palmar articular surface for the os carpi radiale in the radius, and the different proportions of the articular facets for the lateral malleolus and the more acute medial margin of the tibia; as to the calcaneus, its distinctive features are given in figure 1.

Apparently the afrolevantine and central Asian populations of wild camels became separated genetically, perhaps during Lower Pleistocene times, for remains of *C. thomasi* have been recorded from post-Villafranchian, Middle Pleistocene levels (Arambourg 1962). Morphologically the Pleistocene *C. thomasi* represents a dromedary, and the species can therefore be considered a possible ancestor of the domestic one-humped camel.

Toward the end of the Pleistocene C. thomasi became extinct in North Africa, for it is not recorded from Holocene deposits (e.g. Peters 1992), nor is it depicted in Holocene rock art (Muzzolini 1986) from that region. However, a one-humped wild camel likely survived in south-western Asia, as is suggested by rock art (e.g. Anati 1968; Zarins 1989) and bone finds, for example from the pre-pottery neolithic site of Ain el-Assad in the eastern Jordanian desert (Turnbull 1989). The calibrated radiocarbon date of c. 7 200-7 100 yr BC, obtained on a dromedary mandible excavated from a shell midden at Sihi on the Red Sea coast of Saudi Arabia (GRIGSON et al. 1989), apparently was flawed (CLUTTON-BROCK, pers. comm. 1997). Interestingly, the early Holocene camel bones from Ain el-Assad match well with those of modern Arabian camels, whereas the Pleistocene C. thomasi remains came from individuals that surpassed modern domestic animals in size up to 20% or more. Provided that this difference in bone size is not an artefact due to the limited sample size, two explanations can be offered. Perhaps the Holocene finds represent a separate species that developed from C. thomasi or a common ancestor at a much earlier stage. However, this is not visible in the Pleistocene faunal record of southwestern Asia. In fact, none of the "dromedary-sized" camel remains collected from Pleistocene levels in the Levant, submitted for direct radiocarbon dating, proved to be older J. Peters

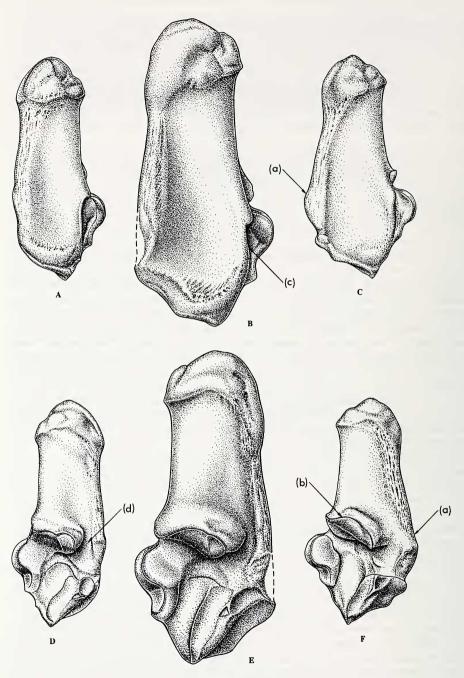


Fig. 1. Calcaneus of Arabian camel (A, D), *Camelus thomasi* (B, E) and Bactrian camel (C, F), lateral and medial view. The distinction between the calcanei of Arabian camel and *C. thomasi* versus Bactrian camel is based on morphological differences in (a) the course of the medioplantar margin, (b) the position of the sustentaculum tali, (c) the lateroplantar margin of the processus coracoideus, and (d) the depth of the sulcus plantar of the sustentaculum tali.

than the 2nd millennium BC (Hedges et al. 1987). An alternative explanation may be that *C. thomasi* underwent a reduction in body size at the transition from the Pleistocene to the Holocene. Such a decrease in body size has been observed in other late Quaternary artiodactyls of the Levant such as wild boar, aurochs, and wild goat (Davis 1987), and it can be assumed that populations of *C. thomasi*, living under similar ecological and/or climatological constraints, were also affected by this phenomenon.

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